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ORIGINAL PAPER

Evaluation of unconstrained and constrained mathematical functions to model girth growth of rubber trees (*Hevea brasiliensis*) using young age measurements

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Abstract: No attempt has been made to date to model growth in girth of rubber tree (*Hevea brasiliansis*). We evaluated the few widely used growth functions to identify the most parsimonious and biologically reasonable model for describing the girth growth of young rubber trees based on an incomplete set of young age measurements. Monthly data for girth of immature trees (age 2 to 12 years) from two locations were subjected to modelling. Re-parameterized, unconstrained and constrained growth functions of Richards (RM), Gompertz (GM) and the monomolecular model (MM) were fitted to data. Duration of growth was the constraint introduced. In the first stage, we attempted a population average (PA) model to capture the trend in growth. The best PA model was fitted as a subject specific (SS) model. We used appropriate error variance-covariance structure to account for correlation due to repeated measurements over time. Unconstrained functions underestimated the asymptotic maximum that did not reflect the carrying capacity of the locations. Underestimations were attributed to the partial set of measurements made during the early growth phase of the trees. MM proved superior to RM and GM. In the random coefficient models, both G_f and G_0 appeared to be influenced by tree level effects. Inclusion of diagonal definite positive matrix removed the correlation between random effects. The results were similar at both locations. In the overall assessment MM appeared as the candidate model for studying the girth-age relationships in *Hevea* trees. Based on the fitted model we conclude that, in *Hevea* trees, growth rate is maintained at maximum value at t_0, then decreases until the final state at $dG/dt \geq 0$, resulting in yield curve with no period of accelerating growth. One physiological explanation is that photosynthetic activity in *Hevea* trees decreases as girth increases and constructive metabolism is larger than destructive metabolism.

Keywords: natural rubber; *Hevea Brasiliensis*; growth modelling; unconstrained functions; constrained functions; mixed model

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Introduction

Hevea brasiliensis (Willd. ex. Adr. de. Juss.) Muell. Arg., is an important industrial tree crop grown mainly in tropical climates up to 12° latitude on both sides of the equator. In India, the crop is largely cultivated between 8°15' N and 12° 52' N latitudes. *Hevea* rubber is the major source of 'natural rubber', a product used in the manufacture of thousands of products of which the pneumatic tyre is the most common. Rubber trees belong to the genus *Hevea* of the family Euphorbiaceae. Though ten species have been recognized in the genus, *H. brasiliensis* is the only species cultivated for obtaining rubber, a product of commercial importance (Webster and Paardekooper 1989). The trees are erect with straight trunks, growing in the wild to over 40 m with a life span of more than 100 years. In managed plantations they rarely exceed 25 to 30 m because tapping reduces growth and trees are usually replanted after 25−30 years when yields fall to an uneconomic level. Most of the modern plantations are raised by clonal buddings on seedling rootstocks. Normally the trees are tapped for latex after 5−8 years of growth and tapping continues for about 20−25 years after which the trees are cut and new plantations are raised. Rubber trees are immature until 6−8 years of age. During this stage, trunk girth measurements and the calculated girth increments are widely used as parameters of growth. The trunk girth and rate of increase in girth are used in experimental work to assess the growth performance of new planting materials and the effects of cultural treatments on growth (Shorrocks et al. 1965; Chandrashekar et al. 1998; Chandrasekhar et al. 2005; Chandrasekhar 2007). Similar to other species, increased girth in *Hevea* can be related directly to the accumulation of dry matter, which reflects the fraction of growth remaining after respiration. Even though domestication of *Hevea* took place more than 150 years ago and *Hevea* is now grown in diverse

environments (Baulkwill 1989), no attempt has been made to fit different growth functions and recommend a suitable model appropriate for the crop.

Biological growth, which is regulated by genetics and environment, changes continuously with age, leading to an increase in volume, size or shape of organism. Several types of age-growth models are widely used to simulate the development of individual trees and to model the dynamics of growth (Ratkowsky 1988; Philip 1994; Vanclay 1994; Seber and Wild 2003). The standard way to study these changes is to fit mathematical functions to growth measurements collected at regular intervals. These functions are explicit expressions of both theory and empirical knowledge and are useful for growth and yield prediction, computation of sustainable yield, and evaluation of alternative management strategies among other uses (El-Shaarawi and Piegorsch 2002). When growth is described by an appropriate function, this can help condense information contained in long data series into a few parameters from which biologically meaningful constants can be derived. From the fitted models, parameters of growth can be derived, including maximum growth potential, maximum rate of change, and site index of clones (a parameter to indicate performance of a clone on a site for a chosen reference age),. These parameters are of importance for assessment of the performance of clones across environments. It is most desirable if these parameters are derived from a set of measurements made during the early growth phase without sacrificing accuracy rather than from a set of size-age measurements from many trees at all ages until the end of the physiologically active life span of the species. The objective of the present study was to evaluate a few widely used growth functions and to identify the most parsimonious and biologically reasonable model that best describes the relationship between girth and age in rubber trees given an incomplete set of young age measurements.

Materials and methods

Study locations, plant material and experimental details

Data for this study were collected from two contrasting locations (L1 and L2). L1 was the headquarters of the Rubber Research Institute of India at Kottayam in Kerala State. L2 was the Rubber Research Institute of India's Regional Research Station at Dapchari in the Thane District of Maharashtra State. The experimental site at L1 was on a hill slope, with Ustic Kanhaplohumults soil of bulk density 1.25 $g \cdot cm^{-3}$, permanent wilting point at 19.7% and field capacity at 27.8%. At L2, data were collected from a clone evaluation trial whose site was slightly undulating. Soil at this site was a clay loam type with bulk density of 1.30 $g \cdot cm^{-3}$, permanent wilting point at 17.5% and field capacity at 30.5%.

The clone used in the study was RRII 105, the clone most widely planted in India. It is a secondary clone produced in India by crossing Tjir 1 and Gl 1 that are primary clones from Indonesia and Malaysia, respectively. Data from L1 were from a trial where 13 modern clones were under evaluation while at L2 15 modern clones were under evaluation. At both locations the trials were laid out using randomized complete block design. The trial at L1 had seven replications with experimental plots of seven plants in a row in contour planting at a spacing of 3.4 m × 6.7 m equivalent to a plant density of 445 $plants \cdot ha^{-1}$. The trial at L2 had three replications with experimental plots of 36 plants in square planting at a spacing of 4 m × 4 m giving a plant density of 638 $plants \cdot ha^{-1}$. Geographical, weather, and soil characteristics of the study locations are given in Table 1. At L1, field planting of the trials was carried out during July/August 1989 while at L2 it was done during 1985. Three whorled plants raised in polyethylene bags (55 cm × 25 cm, lay flat dimension) for five to six months were used for planting. Standard cultural practices, including manuring, weeding, mulching, and sun scorch prevention, were all part of agromanagement (Potty et al. 1980; Pushpadas and Ahmmed 1980; Punnose et al. 2000).

Growth data

Girth measurements made at a fixed height of 1.5 m (the standard in *Hevea* research) from the bud union (collar region) were subjected to modelling. In each month, the measurements were taken during the first three days and were considered as representing the girth of the trees at the end of the previous month. Complete details of the collected growth data are provided in Table 2. At L1 data were collected from February 1989 through January 1997 while at L2 data were collected from February 1991 through January 1997. A total of six years of data from L1 and eight years of data from L2 were used in this study.

Table 1. Geographical, weather and soil characteristics of the study locations

Location	Geographical Latitude (°N)	Longitude (°E)	Altitude (m, asl)	Cultivation zone	Mean annual rainfall (mm)	Wet period (months)	Dry period (months)	Annual range of sunshine duration (h)
Location 1	9.32	76.36	73	Traditional	3500	April to Nov.	Dec. to March	1.7 to 10.2
Location 2	20.04	72.04	48	Non-traditional	2500	June to Sep.	October to May	3.9 to 10.4

Location	Mean annual evaporation (mm/day)	Mean annual minimum temperature (°C)	Mean annual maximum temperature (°C)	Soil Type	Permanent wilting point (%)	Field capacity (%)	Bulk density ($g \cdot cm^{-3}$)
Location 1	3.7	23	31.6	Laterite	19.7	27.8	1.25
Location 2	4.5	20.4	32.7	Clay loam	17.5	30.5	1.3

Table 2. Details of data for analysis from the two locations

Year	Location 1			Location 2		
	Remarks	Age	Number of years for which data is available	Remarks	Age	Number of years for which data is available
1985				Year of planting	1	
1986					2	
1987					3	
1988					4	
1989	Year of planting	1		Start of data collection	5	1
1990		2		---	6	2
1991	Start of data collection	3	1	---	7	3
1992	---	4	2	---	8	4
1993	---	5	3	---	9	5
1994	---	6	4	---	10	6
1995	---	7	5	---	11	7
1996	---	8	6	---	12	8
1997	●January was the end point of girth recording ●Tapping started from March			●January was the end point of girth recording ●Tapping started from October		

Growth functions used

Many mathematical models are used to describe the growth of plants and animals over time. The models are based on general deterministic differential equation of the form dy/dt=f(y,t). Growth functions used in this study are the Richards, Gompertz and monomolecular. These functions belong to the exponential decline family of growth models that seek biological interpretation. Basic constructs of the functions and their mathematical properties are given in Table 3. In all three models G is the observed girth at age **t** (expressed in this study in years), $\mathbf{G_f}$ is the asymptotic limit when t approaches infinity and it indicates the maximum possible value of the dependent variable determined by the productive capacity of the site. '**m**' in the Richards model is the dimensionless shape parameter that permits a variable point of inflection. "**k"** is a function of the ratio of maximum growth rate to mature size, normally referred to as maturing rate. It serves both as a measure of growth rate and of rate of change in growth rate. Parameter "**b"** has no specific biological meaning and it positions the curve in relation to the time axis (origin of the growth curve). In this study, models were reparameterized in terms of G_0= $G(t_0)$ for some t_0 were used (Seber and Wild 2003; Thornley and France 2007). The models were:

Richards (RM_U) as:

$$G = \left(G_f^{(1-m)} - (G_f^{(1-m)} - G_0^{(1-m)})e^{-k(t-t_0)}\right)^{\frac{1}{(1-m)}}$$

Gompertz (GM_U) as: $G = G_f e^{\left[-\ln\left(\frac{G_f}{G_0}\right)\right]e^{-k(t-t_0)}}$

Monomolecular (MM_U) as: $G = (G_f - (G_f - G_0)e^{-k(t-t_0)})$

These reparameterized models were preferred over basic forms because specific meanings could be assigned to each of the parameters. The Gompertz equation assumes that the substrate is non-limiting and quantity of growth machinery is proportional to G with inflection point fixed at $\frac{G_f}{e}$. Monomolecular model is the least complex of the equations that describe the progress of growth in a simple, irreversible first order reaction. The model possesses only an asymptote and intersects the time axis but it has no inflection point. This curve rises rapidly during the initial period and the instantaneous growth rate decreases monotonically to approach asymptotically some final value.

Table 3. Basic forms of the functions used in the study and their mathematical properties

Property	Functions		
	Richards (RM)[1]	Gompertz (GM)[2]	Monomolecular (MM)[1]
Equation	$G = G_f\left(1 - be^{-kt}\right)^{\frac{1}{1-m}}$	$G = G_f e^{-be^{-kt}}$	$G = G_f\left(1 - be^{-kt}\right)$
No. of constants	4	3	3
Growth rate (1st Derivative)	$\frac{dG}{dt} = \eta G^m - kG$	$\frac{dG}{dt} = kG \log\frac{G_f}{G}$	$\frac{dG}{dt} = k(G_f - G)$
Asymptotes - Lower	For $m > 0$ both are asymptotes, but for $m < 0$ there is no lower asymptote and no point of inflection	0	nil (crosses t-axis)
Upper		G_f	G_f
Curve shape symmetry	Asymmetrical	Asymmetrical	Concave
Inflection point	$G_f m^{\frac{1}{1-m}}$	$\frac{G_f}{e}$	Absent
Maximum growth rate	$G_f k m^{\frac{m}{1-m}}$	$k\frac{G_f}{e}$	Occurs in the beginning

[1](Richards, 1959); [2](Winsor, 1932; Richards, 1959)

Constraining of functions

When the models were fitted using unconstrained functions, the models underestimated the asymptotic maximum that did not reflect the carrying capacity of the locations. Published research suggests constrained modelling to circumvent the problem of underestimation (Shifley and Brand 1984; Salas and Garcia 2006). In this study, constraint was put on growth duration (T). From previous experience in typical commercial situations, untapped bud-grafted trees take a growth duration (T) of about 25 to 30 years to attain asymptotic maximum growth (Joseph G. Marattukalam, Retired Scientist, Marattukalam House, 225 Aramanapady, Chenganachery-686101, Kerala, India, personal communication). A higher range of T= 30 years was considered in this study to allow trees to reach their potential size determined by genetic and environmental factors. The constraint was introduced into the growth functions by replacing the rate constant 'k' in the equations by a rearranged formula that is used for working out duration of growth (T) which is a function of 'k'. This was a simple extension of the ideas that have been used to solve for various growth quantities (Richards 1959). The formulas were: k=(2m+2)/T, for the Richards model, k=4/T, for the Gompertz model and k=2/T, for the Monomolecular model. Constructs of the equations used for the re-parameterized constrained models were:

Richards (RM_C) as:

$$G = (G_f^{(1-m)} - (G_f^{(1-m)} - G_0^{(1-m)})e^{-\left(\frac{2m+2}{T}\right)(t-t_0)})^{\frac{1}{(1-m)}}$$

Gompertz (GM_C) as:

$$G = G_f e^{\left[-\ln\left(\frac{G_f}{G_0}\right)\right] e^{-\frac{4}{T}(t-t_0)}}$$

Monomolecular (MM_C) as:

$$G = (G_f - (G_f - G_0)e^{-\frac{2}{T}(t-t_0)})$$

Statistical analyses

All modelling work was undertaken at the location level using the individual tree measurements from all the replicate plots. Only tree level structure was considered and the plot level structure was ignored. Data analyses were carried out in the open source software R, a free software environment for statistical computing and graphics (R-development core team 2010). A two-stage approach was adopted. In the first stage, growth was modelled to capture the time trend around a population average (PA) model wherein the parameters of the function are assumed to be invariant across the trees (i.e., fixed). Fittings of functions were carried out using the nlstools package (Delignette-Muller and Baty 2010). Starting values for all the parameters were specified following Fekedulegn et al. (1999), Ogle (2010). Value of t_0 was fixed at 7, as this is the standard age for deciding the tappability of *Hevea* plantations (G_0 at t_0=7) for latex harvesting. This also helped in comparison of predicted girth at that age in different models. Starting values were first evaluated in the function preview of the nlstools package with repeated modifications to reach a good approximation of estimates which were then used for fitting the model in the nlstools package (Delignette-Muller and Baty 2010). Statistical significance of the parameters of the nonlinear models was determined by evaluating the 95% asymptotic confidence intervals (ACI) of the estimated parameters. The null hypothesis (H_0) that the parameter in question is not significantly different from zero was rejected when the 95% ACI of the parameter did not include zero.

General goodness of fit of the fitted models were evaluated using adjusted proportion of variation (R^2_{adj}), residual sum of squares (RSS), Akike information criterion (AIC), Bayesian information criterion (BIC) and Model Selection Criterion (MSC, *Scientist* software, Micromath, Saint Louis, Missouri, USA). Using AIC and BIC values, the more appropriate model was judged as the one with smaller values. The decisions rule with MSC is that the model with larger MSC is the more appropriate one. Validity of the assumptions of the error model was checked by plotting non-transformed residuals against fitted values. Bootstrap (with 2000 iterations) sampling was also performed to validate the model parameter estimates following Delignette-Muller and Baty (2010).

In the second stage mixed model analysis was attempted to fit a subject specific (SS) model (random coefficient regression model) allowing for individual differences G_f and G_0. This analysis was restricted only to the PA model selected in the first stage. Usually forest growth and yield data exhibit both heteoscedasticity and autocorrelation (Gregoire et al. 1987). As the data used in this study are repeated measurements over time, it is expected that measurements on the same tree made near in time would be more highly associated than measurements made further apart in time. To account for this variation, different error variance-covariance structures were tried but only the relevant and helpful ones are shown and discussed here as the other methods did not yield useful results that warranted presentation. These analyses were carried out following Gregoire et al. (1987), Vonesh and Chinchilli (1997) and Pinheiro and Bates (2000).

Results

Unconstrained/constrained models

Fitting results of the unconstrained functions (Table 4) revealed that parameter estimates for all the functions are significant at α = 0.05. Model fittings of L1 yielded the lowest estimate for G_f in GM_U, the highest estimate in MM_U and an intermediate in RM_U. The range of 95% ACIs was similar for RM_U and MM_U but in GM_U it was small. Estimates of G_0, ASEs, and 95% ACIs were similar for all models. The estimate of *m* in RM_U was a positive value with a very high correlation with G_f. RMSE, R^2_{adj} and MSCs were almost similar. L2 yielded the highest value in RM_U,

lowest in GM_U and was intermediate in MM_U. Asymptotic error and range of 95% ACI was highest in RM_U while they were similar in the other two models. Estimates of G_0 were similar in all models. At L2, *m* in RM_U was negative with a very high correlation with G_f. Other fit statistics were almost similar except for GM_U where AIC and BIC values were higher. The trajectory of the fitted curve appeared more realistic in the scatter plots of girth of trees overlaid with fitted curves (Fig. 1). Residual plots (Fig. 2) did not reveal any non-randomness in errors as they were more or less uniformly distributed on either side of mean zero.

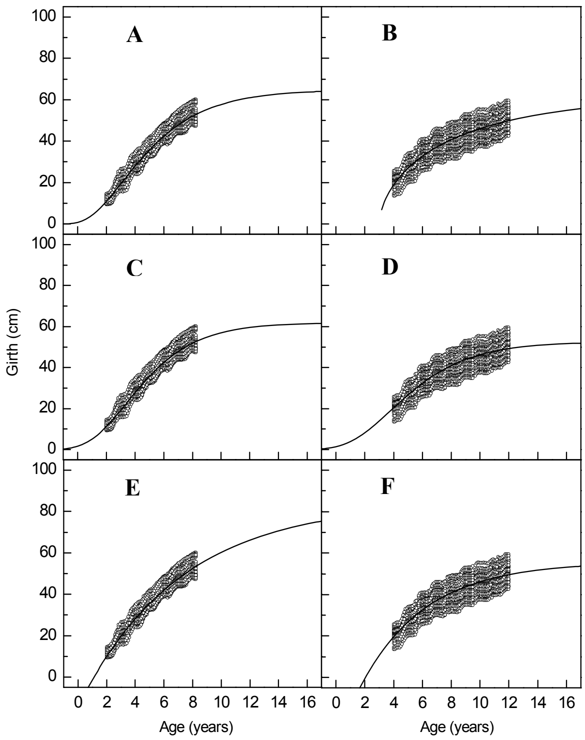

Fig. 1 Scatter plot of girth of trees overlaid with function plots of unconstrained RM (A, B), GM (C, D) and MM (E, F) models fitted to data from two locations L1 (A, C, E) and L2 (B, D, F)

In the results from constrained models (Table 5), the maximum estimate was obtained in GM_C, the minimum in MM_C and an intermediate in RM_C for L1. ASE and range of 95% ACI was lowest for MM_C while in the other two they were higher. Estimates, ASE's, and 95% ACI's for G_0 were almost similar in all the models. Estimate of *m* was negative with very high correlation with G_f. While AIC's and BIC's were high for GM_C, they were lower for RM_C and intermediate for MM_C. Other diagnostic parameters were comparable. For L2, RM_C did not converge to a solution in spite of various combinations of starting values. Parameter estimates and diagnostic statistics of the other two models indicated better characteristics in MM_C. Trajectory of the fitted curves was more realistic in MM_C (Fig. 3) while the residual plots (Fig. 4) did not reveal any non-randomness in errors except in GM_C. Bootstrap estimates of the parameters (Tables 6) were comparable with the respective model parameters.

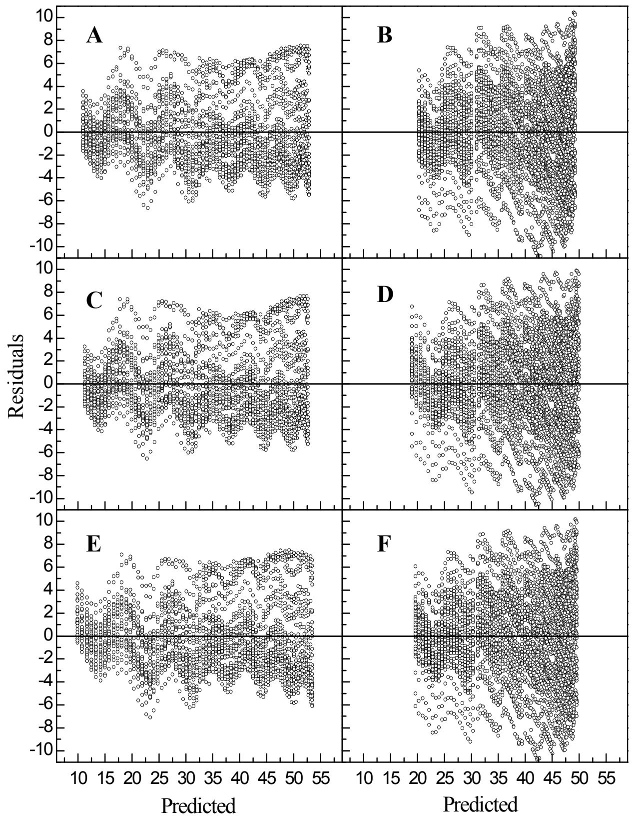

Fig. 2 Scatter plot of residuals against predicted values of the unconstrained RM (A, B), GM (C, D) and MM (E, F) models fitted to data from two locations L1 (A, C, E) and L2 (B, D, F)

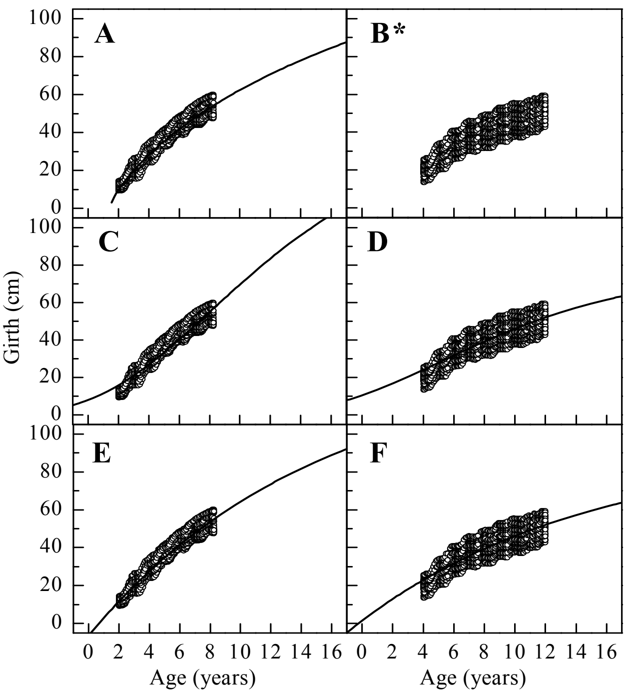

Fig. 3 Scatter plot of girth of trees overlaid with function plots of constrained RM (A), GM (C, D) and MM (E, F) models fitted to data from two locations L1 (A, C, E) and L2 (D, F). *RM model for this location did not converge to a solution and hence no overlaid function plot (Refer Table 5)

Table 4. Parameter estimates and goodness of fit statistics of the unconstrained models fitted to *Hevea* girth data from two locations

Location		G_f (cm) Estimate	ASE	95% ACI (L)	95% ACI (U)	G_0 (cm) Estimate	ASE	95% ACI (L)	95% ACI (U)	*k* Estimate	ASE	95% ACI (L)	95% ACI (U)	*m* Estimate
	RM_U	64.86	2.05	60.85	68.88	47.74	0.09	47.54	47.93	0.31	0.03	0.25	0.38	0.73
Location (L1)[a]	GM_U	61.92	0.6	60.74	63.1	47.8	0.09	47.62	47.98	0.38	0.01	0.36	0.39	--
	MM_U	84.37	2.14	80.17	88.57	47.56	0.09	47.38	47.73	0.14	0.01	0.13	0.15	--
	RM_U	61.82	3.06	55.82	67.81	37.14	0.09	36.97	37.32	0.13	0.03	0.07	0.18	-0.85
Location (L2)[b]	GM_U	52.56	0.34	51.9	53.22	37.12	0.09	36.94	37.31	0.34	0.01	0.32	0.35	--
	MM_U	55.69	0.52	54.66	56.71	37.16	0.09	36.98	37.34	0.22	0.01	0.21	0.24	--

Location		ASE	95% ACI (L)	95% ACI (U)	Correlation between G_f & G_0	G_f & *k*	G_f&*m*	Fit Statistics	RMSE		LL	AIC	BIC
	RM_U	0.15	0.45	1.02	-0.2	-0.98	-0.93	RMSE		LL	AIC	BIC	MSC
Location (L1)[a]	GM_U	--	--	--	0.38	-0.95	--	3.15	0.94	-6633.02	13276.04	13305.33	2.84
	MM_U	--	--	--	0.31	-0.99	--	3.16	0.94	-6634.52	13277.05	13300.48	2.84
	RM_U	0.26	-1.35	-0.35	-0.32	-0.99	-0.94	3.17	0.94	-6646.79	13301.59	13325.02	2.83
Location (L2)[b]	GM_U	--	--	--	-0.64	-0.93	--	3.92	0.83	-12558.02	25126.03	25158.1	1.76
	MM_U	--	--	--	-0.69	-0.97	--	3.94	0.83	-12584.51	25177.03	25202.68	1.75
								3.92	0.83	-12564.33	25136.65	25162.31	1.76

ASE = asymptotic standard error; ACI = asymptotic confidence interval; L = lower; U = upper. RMSE = Residual mean square error; LL = Log likelihood; AIC = Akike information criterion; BIC = Bayesian information criterion; MSC = model selection criterion. [a]n = 34 trees, 76 cases tree^{-1}; [b]n= 48 trees, 94 cases tree^{-1}

Table 5. Parameter estimates and goodness of fit statistics of the constrained models fitted to Hevea girth data from two locations.

Parameter/Statistic		Location (L1)[a] RM_C	Location (L1)[a] GM_C	Location (L1)[a] MM_C	Location (L2)[b] RM_C	Location (L2)[b] GM_C	Location (L2)[b] MM_C
G_f (cm)	Estimate	148.69	151.07	138.84		77.93	93.18
	ASE	1.73	1.41	0.53		0.42	0.40
	95% ACI (L)	145.30	148.30	137.79		77.11	92.40
	95% ACI (U)	152.09	153.84	139.88		78.75	93.96
G_0 (cm)	Estimate	47.51	47.53	47.72		35.50	35.70
	ASE	0.09	0.11	0.09		0.07	0.07
	95% ACI (L)	47.33	47.31	47.54		35.36	35.57
	95% ACI (U)	47.69	47.74	47.89		35.64	35.83
k^c	Estimate	0.04	0.13	0.07	The model did not converge to a solution in spite of various combinations of starting values	0.13	0.07
m	Estimate	-0.36	--	--		--	--
	ASE	0.03	--	--		--	--
	95% ACI (L)	-0.43	--	--		--	--
	95% ACI (U)	-0.29	--	--		--	--
Correlation between G_f & G_0		-0.09	0.63	0.79		-0.36	-0.19
G_f & *m*		-0.96	--	--		--	--
Fit Statistics							
RMSE		3.20	3.84	3.26		4.23	4.13
R^2_{adj}		0.94	0.91	0.94		0.80	0.81
LL		-6667.86	-7144.24	-6721.75		-12906.43	-12802.77
AIC		13343.73	14294.48	13449.49		25818.86	25611.55
BIC		13367.16	14312.05	13467.07		25838.10	25630.79
MSC		2.82	2.45	2.77		1.61	1.66

ASE = asymptotic standard error; ACI = asymptotic confidence interval; L = lower; U = upper. RMSE = Residual mean square error; LL = Log likelihood; AIC = Akike information criterion; BIC = Bayesian information criterion; MSC = model selection criterion. [a]n = 34 trees,76 cases tree^{-1}; [b]n = 48 trees, 94 cases tree^{-1}. [c]Back calculated value based on the parameter's relationship with duration of growth (T) as k = (2m+2)/30 for Richards, k = 4/30 for Gompertz and k = 2/30 for Monomolecular.

Table 6. Bootstrap estimates of model parameters of the unconstrained and constrained functions fitted to *Hevea* girth data from two locations

Location		Unconstrained model											
		G_f (cm) Estimate	95% BCI (L)	95% BCI (U)	G_0 (cm) Estimate	95% BCI (L)	95% BCI (U)	*k* Estimate	95% BCI (L)	95% BCI (U)	*m* Estimate	95% BCI (L)	95% BCI (U)
Location (L1)[a]	RM	64.88	61.5	69.41	47.73	47.54	47.93	0.31	0.25	0.38	0.73	0.47	1.03
	GM	61.94	60.85	63.14	47.8	47.62	47.98	0.38	0.36	0.39	--	--	--
	MM	84.41	80.59	88.75	47.56	47.38	47.74	0.14	0.13	0.15	--	--	--
Location (L2)[a]	RM	61.7	57.3	70.85	37.14	37	37.31	0.13	0.07	0.19	-0.84	-1.31	-0.34
	GM	52.57	51.92	53.23	37.13	36.95	37.3	0.34	0.32	0.35	--	--	--
	MM	55.7	54.74	56.76	37.16	37	37.35	0.22	0.21	0.24	--	--	--

Location		Constrained model								
		Gf (cm) Estimate	95% BCI (L)	95% BCI (U)	G_0 (cm) Estimate	95% BCI (L)	95% BCI (U)	*m* Estimate	95% BCI (L)	95% BCI (U)
Location (L1)[a]	RM	148.71	145.55	152.3	47.51	47.33	47.69	-0.36	-0.42	-0.3
	GM	151.07	148.33	153.78	47.52	47.32	47.75	--	--	--
	MM	138.84	137.82	139.91	47.72	47.54	47.9	--	--	--
Location (L2)[a]	RM	--	--	--	--	--	--	--	--	--
	GM	77.92	77.1	78.78	35.5	35.36	35.65	--	--	--
	MM	93.17	92.39	93.94	35.7	35.57	35.82	--	--	--

BCI = bootstrap confidence interval (with 2000 iterations); L = lower; U = upper. [a]n = 34 trees and 76 cases tree^{-1} in L1 and 48 trees and 94 cases tree^{-1} in L2.

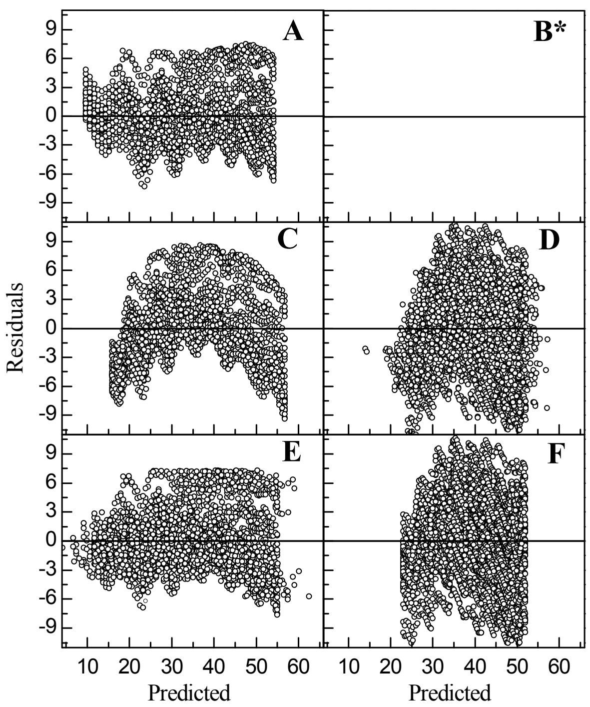

Fig. 4 Scatter plot of residuals against predicted values of the constrained RM (A), GM (C, D) and MM (E, F) models fitted to data from two locations L1 (A, C, E) and L2 (D, F) [*RM model for this location did not converge to a solution and hence no plot of residuals (Refer Table 5)]

Mixed models

In the mixed modelling approach (Tables 7 and 8), inclusion of random effects in both G_f and G_0 resulted in significant reduction in RMSE, but did not result in removing the correlation between them. Addition of diagonal positive definite matrix to account for the variance-covariance structure of the random terms not only resulted in significant reduction in RMSE but also removed the correlation between G_f and G_0. The results were similar for both locations. Further, addition of variance and correlation structures did not result in significant improvement in model fittings. The residual plots of the models (Fig. 5) did not reveal any non random (systematic) distribution of errors but a seasonal component was evident. Growth profiles of the trees predicted for a growth period of 30 years (Fig. 6) using constrained random coefficient model (mixed model) indicated the superiority of L1 for the studied clone. Comparison of growth trajectory profiles of trees from both locations indicated that trees at L2 would take two to two and a half years more to attain the standard girth necessary for a decision to tap trees.

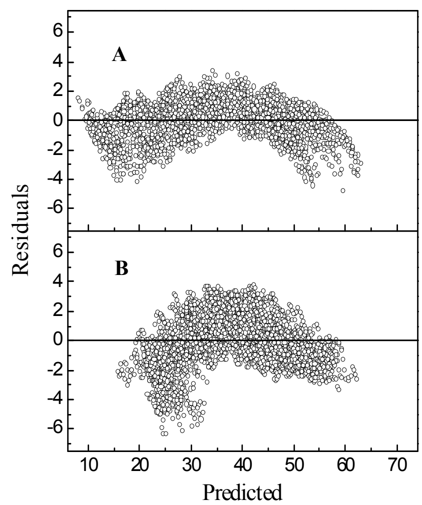

Fig. 5 Scatter plot of residuals against predicted values of the constrained random coefficient MM model fitted to data from two locations L1 (A) and L2 (B).

Table 7. Comparison of mixed-effects model performance with tree-level random effects components and different variance-covariance structures for the constrained monomolecular model (MM_C) fitted to *Hevea* girth data for location 1.

Specification	Model	df	AIC	LL	RMSE	r (G_f vs. G_0)	*P* |LRT|
All parameters fixed	M1	3	13449.49	-6721.75	3.26	0.79	--
Random effect in G_f	M2	4	12916.3	-6454.15	2.88	--	--
M2 vs. M1	--	--	--	--	--	--	0.001
Random effects in G_f & G_0	M3	6	9166.98	-4577.49	1.34	0.914	--
M2 vs. M3	--	--	--	--	--	--	0.001
Variance –Covariance for random terms							
M3 + Diagonal positive-definite matrix	M4	5	9221.27	-4605.63	1.34	0.005	--
M3 vs. M4	--	--	--	--	--	--	0.001
M3 + General positive-definite matrix	M5	6	9614.72	-4576.36	1.34	0.914	--
M4 vs. M5	--	--	--	--	--	--	0.001
Variance structure for residuals							
M4 + Power of a variance covariate	M6	6	9222.92	-4605.46	1.22	0.006	--
M4 + Exponential of a variance covariate	M7	6	9164.72	-4576.36	1.34	0.912	--
M6 vs. M7	--	--	--	--	--	--	ns
Correlation structure for residuals							
M4 + Autoregressive process of order 1 (AR1)	M8	6	4229.6	-2108.8	3.32	0.649	--
M4 + Continuous autoregressive process (AR1) for a continuous time covariate (CAR1)	M9	6	4229.6	-2108.8	3.32	0.649	--

df = degrees of freedom; AIC = Akike information criterion; LL = Log likelihood; RMSE = Residual mean square error; r = correlation coefficient; *P* |LRT| = probability of likelihood ratio test. ns = not significant.

Table 8. Comparison of mixed-effects model performance with tree-level random effects components and different variance-covariance structures for the constrained monomolecular model (MM_C) fitted to *Hevea* girth data for location 2.

Specification	Model	df	AIC	LL	RMSE	r (G_f vs. G_0)	*P* |LRT|
All parameters fixed	M1	3	25611.55	-12802.77	4.13	-0.19	--
Random effect in G_f	M2	4	24587.85	-12289.93	3.62	-0.036	--
M2 vs. M1	--	--	--	--	--	--	0.001
Random effects in G_f & G_0	M3	6	17828.09	-8908.55	1.66	0.786	--
M2 vs. M3	--	--	--	--	--	--	0.001
Variance –Covariance for random terms							
M3 + Diagonal positive-definite matrix	M4	5	17873.27	-8931.64	1.66	-0.001	--
M3 vs. M4	--	--	--	--	--	--	0.001
M3 + General positive-definite matrix	M5	6	17829.09	-8908.55	1.66	0.786	--
M4 vs. M5	--	--	--	--	--	--	0.001
Variance structure for residuals							
M4 + Power of a variance covariate	M6	6	16898.34	-8443.17	16.77	-0.006	--
M4 + Exponential of a variance covariate	M7	6	16898.34	-8443.17	16.77	-0.006	--
M6 vs. M7	--	--	--	--	--	--	ns
Correlation structure for residuals							
M4 + Autoregressive process of order 1 (AR1)	M8	6	6379.97	-3183.98	4.09	0.329	--
M4 + Continuous autoregressive process (AR1) for a continuous time covariate (CAR1)	M9	6	6379.97	-3183.98	4.09	0.329	--

df = degrees of freedom; AIC = Akike information criterion; LL = Log likelihood; RMSE = Residual mean square error; r = correlation coefficient; *P* |LRT| = probability of likelihood ratio test. ns = not significant.

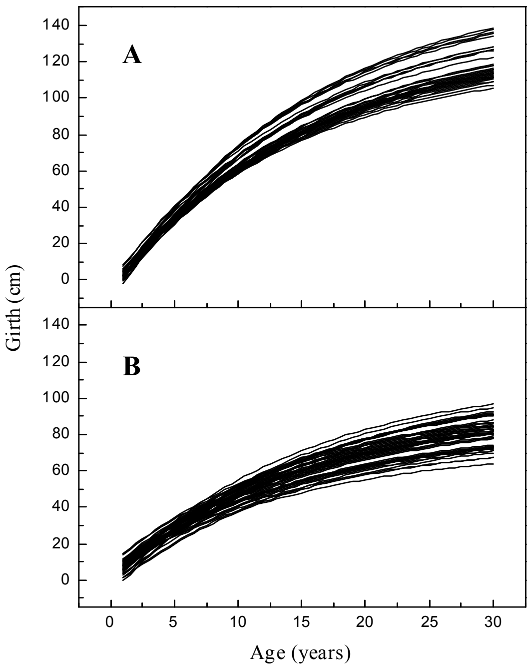

Fig. 6 Growth profiles of *Hevea* trees predicted for a growth period of 30 years using the constrained random coefficient MM model for the two locations L1 (A) and L2 (B).

Discussion

Fixed effects models

Unconstrained functions underestimated the asymptotic maximum that did not reflect the carrying capacity of the locations. This was expected because close to reality estimations are possible only from a set of size-age measurements at every age until the attainment of plateau at maturity. The underestimations were due to partial sets of measurements made in the early growth phase of the trees. It has been observed at L1 that untapped trees of clone RRII 105 attain 130 to 140 cm of girth after about 30 years of growth (J. G. Marattukalam, (personal communication, 2010). Underestimations can easily be attributed to the partial set of measurements made in early growth phase of the trees. Before settling on constraining (T), the option of constraining G_f was considered and was discounted as inappropriate as it would not bring out productivity differences between the study sites. Constraining duration of growth was the best option because it was possible to approximate a bench mark value for obtaining maximum potential growth that would not exceed the biologically reasonable limits. Further, it was assumed that given a range of environments where rubber is being grown, fixing a bench mark value for the duration of growth would be prudent in standardizing it for future studies. In addition, holding the growth period constant would enable more meaningful comparison of all growth quantities within, between, and among clones and locations.

Results from both unconstrained and constrained models indicated superiority of RM and MM compared to GM. Though RM yielded a fit as good as did MM, a slight edge of RM over MM was expected as the curve generated by an equation with more variables will nearly always have better diagnostic statistics simply because it has additional parameters. In RM estimate of parameter **m** was inconsistent between unconstrained and constrained models both in sign and magnitude. While in RM_U its value was positive for L1, negative for L2, but in RM_C it was negative for L1 and the model did not converge for L2. The correlation with G_f and **m** was also high indicating the redundancy of the parameter. Further, negative values of **m** indicate absence of a lower asymptote and the inflection point, which are characteristic of the MM curve (Richards 1959; Rose & Charles-Edwards 1981; Zhao-gang & Feng-ri 2003; Lei & Zhang 2004). It has been reported that the Richards function will not fit sets of data which show insufficient curvature towards an upper asymptote (Hunt 1982). Further, Fekedulegn et al. (1999) reported that investigations of the differential forms and second derivatives of the equation have indicated the unsuitability of the function to model data that does not encompass the entire range of the life cycle (i.e., juvenile, adolescent, mature and senescent stages of a biological variable). Some authors consider that the additional parameter used in *RM* has no obvious biological interpretation and it is numerically unstable and often poses problems in fitting the model (Thornley and Johnson 1990; Zeide 1993).

Random effects models

In the random coefficient models, both G_f and G_0 appeared to be influenced by tree level effects. Inclusion of a diagonal positive definite matrix to account for the variance-covariance structure of the random terms removed the correlation between the random effects. The results were similar for both locations. No further improvement could be achieved by including variance modelling to account for heteroscedasticity and within subject correlation in the presence of variance-covariance structures for the random effects. Gregoire and Shabenberger (1996) pointed out that additional within subject correlation is often negligible in the presence of random subject effects.

Overall assessment

In plant growth modelling, the use of fitted curves is of very high importance because the fitted curves can provide the experimenter with a clearer perception of the reality of plant growth when a series of observational data are disturbed by random errors. In most cases the curve is needed not only to provide a convenient re-description of the primary data but as an instrument for derivation of the quantities involved in plant growth analysis (Causton and Venus 1981; Hunt 1982; France and Thornley 1984). In *Hevea*, growth measured in terms of increase in girth of the main stem remains the most important variable of interest to commercial planters and managers. Girth at age seven

is the foremost factor taken into account for evaluating the progress of growth and attainment of maturity for tapping. Girth and rate of girth increase are also used in experimental work to assess the growth performance of new planting materials and effects of cultural treatments on growth (Shorrocks et al. 1965; Chandrashekar et al. 1998; Chandrasekhar et al. 2005; Chandrasekhar 2007).

From my results and discussion it is clear that MM is the preferred candidate model for studying the girth-age relationships in *Hevea* trees. The asymptotic maximum obtained for this model was closer to the observed information for the clone at L1. Additionally, values of allometric parameter m<0 and concave curvature of the scatter plots of observed data also indicate the suitability of MM. Goodness of fit, used alone, could lead to choosing an inappropriate growth function: The extent to which a growth function produces reasonable biological estimates must remain a primary factor in model selection (Vanclay and Skovsgaard 1997; Caillet et al. 2006). This model, though not commonly employed in forest growth studies, is widely used in modelling fast-growing forest trees (Amaro et al. 1998; Zhao-gang & Feng-ri 2003; Lei & Zhang 2004). Thus it appears that in *Hevea* trees, photosynthetic activity decreases as size [G(t)] increases and constructive metabolism exceeds destructive metabolism. As a result, the growth rate is maintained at maximum value at t_0, then decreases until the final stage at $dG/dt \geq 0$ resulting in a yield curve with no period of accelerating growth. The decelerating growth takes place in the beginning and lasts until the final limiting size, G_f (Richards 1959; Zhao-gang & Feng-ri 2003; Lei & Zhang 2004).

Conclusions

The MM model is the most suitable function for study of the increase in girth of *Hevea* trees. Further, for subject specific modelling, inclusion of a diagonal positive definite matrix to account for the variance-covariance structure of the random terms would take care of both heteroscedasticity and within subject correlation in the repeated measures. The model presented is a generic one ignoring the influences of various other factors. Testing of this model utilising data from contrasting climatic conditions and incorporation of modifier functions of weather factors into the growth equation should yield more information on the utility of the function to model *Hevea* growth. Further studies are in progress to incorporate seasonality of growth (both wet and dry seasons), clonal variation, site index (that reflect the nutrient availability and average climatic conditions), environmental influences (rainfall, temperature, relative humidity, soil factors, and others) and management practices (plating density, fertilisation regimes, and others) in the growth model.

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